MADROÑO, Vol. 61, No. 3, pp. 276–289, 2014

THE ROLE OF SOIL CHEMISTRY IN THE GEOGRAPHIC DISTRIBUTION OF *CEANOTHUS OTAYENSIS* (RHAMNACEAE)

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ABSTRACT

Ceanothus otayensis McMinn (Rhamnaceae) was previously known only from metavolcanic-derived soils of the northern Peninsular Ranges—predominantly the San Ysidro Mountains—in San Diego County, California, and adjacent Baja California, Mexico. Recently, a new population of *C. otayensis* was discovered on sedimentary soils at Marine Corps Air Station Miramar, 25 km northwest of the next nearest known population. Sedimentary deposits at the new locality are thought to produce unusual soils. It is possible that the disjunct distribution of *C. otayensis* is a response to soil conditions, a phenomenon frequently seen in other members of *Ceanothus*, for instance on serpentine. The present study uses soil chemistry data for seven populations and subpopulations of *C. otayensis* (metavolcanic: n = 5; sedimentary: n = 2), as well as 22 populations of closely related *Ceanothus*, to determine whether soils of *C. otayensis* are chemically distinct from those of closely related *Ceanothus*, and answer the following question: are sedimentary-derived soils at the new locality chemically similar to metavolcanic-derived soils that support all other known populations of the species? Soils of *C. otayensis* proved to be chemically distinct from soils of closely related *Ceanothus*, with significantly lower levels of nitrate, sulfur, and conductivity. Sedimentary and metavolcanic soils of *C. otayensis* proved to be chemically indistinguishable from one another ($P < 0.05$), with low levels of all assayed nutrients other than Ca, suggesting a chemical similarity among the soils of *C. otayensis* that may help explain its disjunct distribution. Population size estimates indicate that the new disjunct locality at Marine Corps Air Station Miramar supports about 75 adult individuals.

Key Words: California, ecology, edaphic, metavolcanic, Mexico, Miramar, Otay Mountain.

Plant-soil interactions are a primary driver of plant distribution, as well as a potentially potent force in plant evolution (Stebbins 1942; Kruckeberg 2002; Kay et al. 2011). Unusual soils—such as serpentine—have long been known to support unusual plant communities, including many species that are endemic to such soils, and likely specialized via local adaptation (Gankin and Major 1964; Kruckeberg 1986; O'Dell and Rajakaruna 2011). Although several such "edaphic endemic" taxa have been examined using modern soil chemistry and experimental tools (Baldwin 2005; Sambatti and Rice 2006; Burge et al. 2013), little is presently known about how soil conditions influence adaptation and geographic distribution in such plants, particularly those that are specialized to soils other than serpentine. By examining specific cases of edaphic endemism using soil chemistry data, it may be possible to discern general trends in the evolution and maintenance of soil associations in edaphically specialized species or plant communities.

The present contribution focuses on *Ceanothus otayensis* McMinn, a member of *Ceanothus* subgenus *Cerastes* S. Wats. *Ceanothus otayensis* is a low-stature, ascending shrub that is morphologically similar to *Ceanothus perplexans* Trel. and *Ceanothus crassifolius* Torr. (Boyd and Keeley 2002), and was once thought to have arisen via hybridization between these two species (McMinn 1942). However, neither of the putative parent species is present within the geographic range of *C. otayensis*, and genetic evidence does not support a hybrid origin (Burge et al. 2011).

Ceanothus otayensis was previously thought to occur only on metavolcanic-derived soils of the Peninsular Ranges in southern San Diego County, California, and adjacent Baja California, Mexico (McMinn 1942; Wilken 2006). *Ceanothus otayensis*, along with a small group of species endemic to the San Ysidro Mountains, has been treated as a specialist on metavolcanic-derived soils. Such soils are thin, extremely rocky, and very fast-draining (Bowman 1973). However, very little research has focused on the chemical and physical properties of these soils, or their potential influence on plant life.

During a visit to the San Diego Natural History Museum, the author came upon a specimen of *C. otayensis* collected at Marine Corps Air Station Miramar (hereafter MCAS Miramar; *Roberts & Dossey 6209*; Appendix 1), 25 km to the northwest of the next nearest known population (Figs. 1 and 2). In 2009, the author visited the locality and was able to locate a small population of these plants (estimated at the time

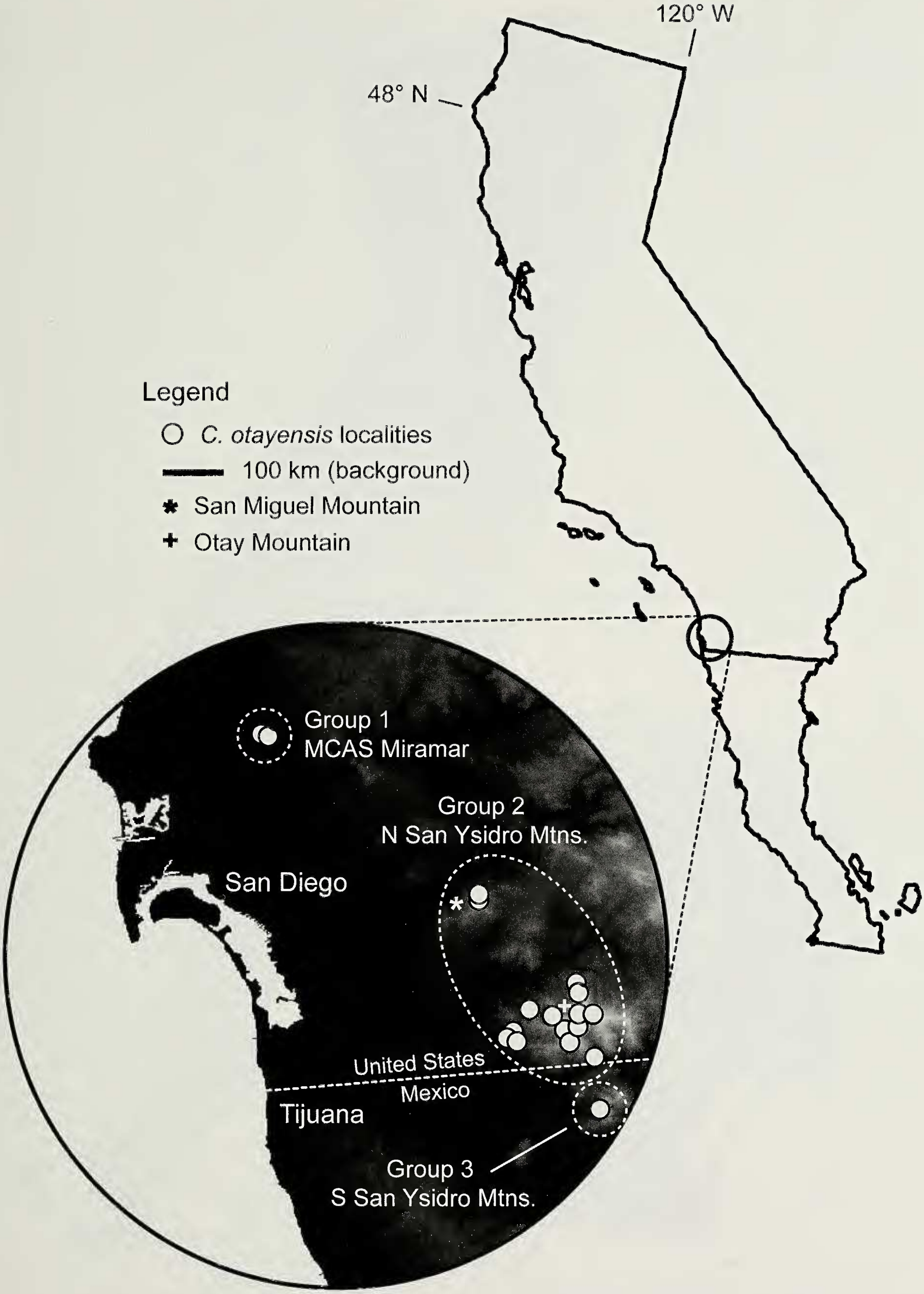

FIG. 1. Global distribution of *C. otayensis*. Locality data for *C. otayensis* taken primarily from the Consortium of California Herbaria (http://ucjeps.berkeley.edu/consortium); additional data from Jon Rebman (personal communication); only unique localities mapped (Appendix 2). Inset map of topography is from Jarvis et al. (2008).

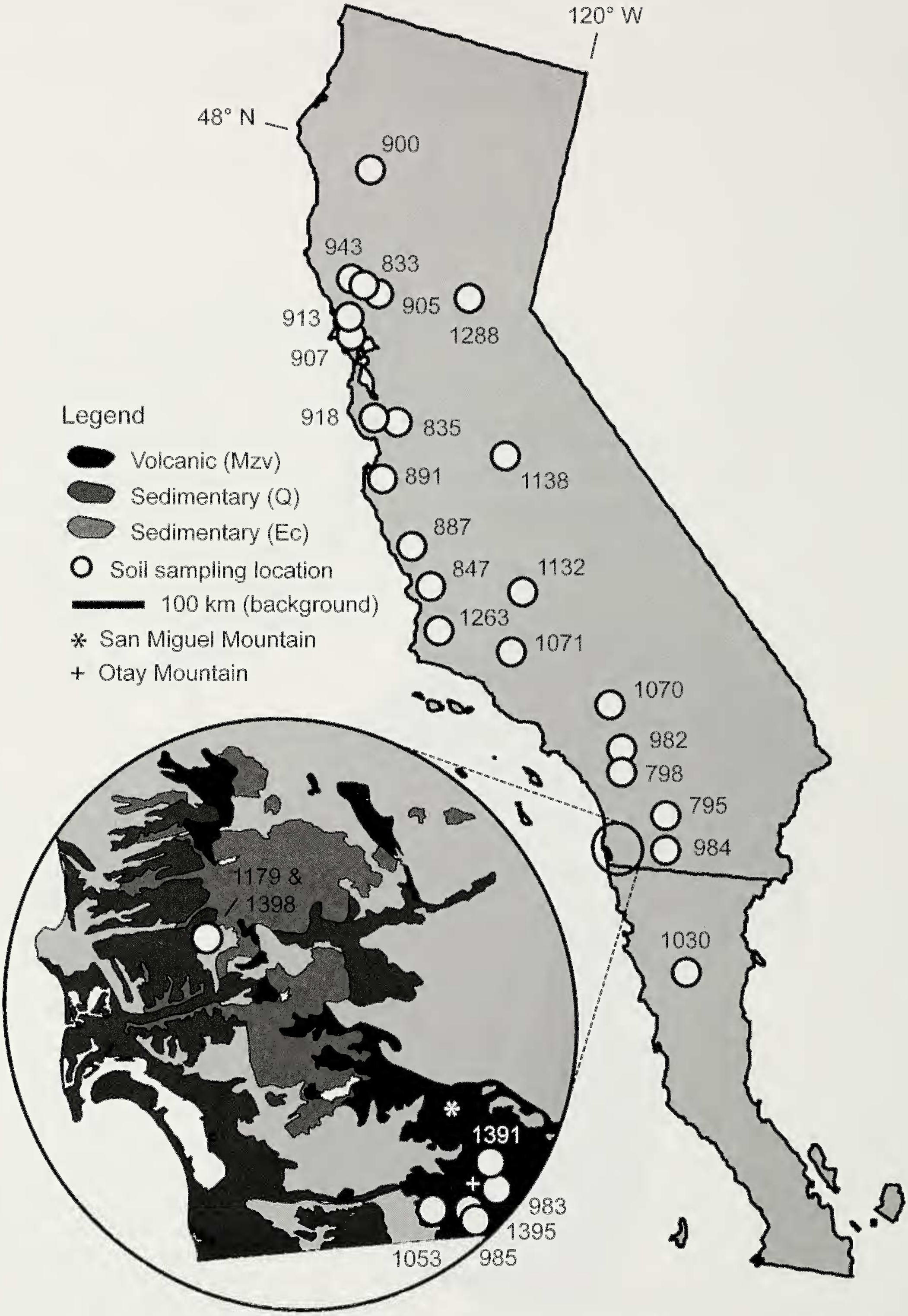

FIG. 2. Sampling and soil map. Soil sampling locations indicated by open circles (Table 2). Inset map shows *C. otayensis* sampling in San Diego County; polygons for soils adapted from GIS layers in Soil Survey Geographic (SSURGO) database for San Diego County (USDA 2007).

to contain less than 100 individuals) on sedimentary slopes of upper San Clemente Canyon on Kearney Mesa (*Burge 1179*; Appendix 1). The presence of *C. otayensis* on low-elevation (130 m) sedimentary-derived soils at MCAS Miramar suggests that the plant may not be a soil specialist, as previously assumed.

The present study uses chemical analysis of soils to answer two outstanding questions on the soil chemistry associations and distribution of *C. otayensis*: 1) Are the soils occupied by *C. otayensis* chemically distinct from those occupied by other members of *Ceanothus* subgenus *Cerastes* in California? and 2) Are the sedimentary-derived soils at the new MCAS Miramar locality chemically similar to the metavolcanic-derived soils that support other known populations of *C. otayensis*? Population size estimates for *C. otayensis* at MCAS Miramar are also presented, and conservation implications for this rare species are discussed.

Materials and Methods

Determining Geological Formations and Soil Types

To determine the general soil and geology associations of *C. otayensis*, a GIS approach was applied to available georeferenced specimens of the species. Occurrence data for sites other than those reported by DOB (Appendix 1) were obtained from the Consortium of California Herbaria (CCH 2013). Records were selected only if they explicitly provided latitude and longitude data on the label. Duplicates were removed using location; records with the same location—based on latitude and longitude rounded to three decimal places—were removed, resulting in a list of high-quality localities (Appendix 2).

Geological formations and soil types at individual sites were determined using a GIS approach, combined with reference to the geological and soil literature. Latitude and longitude data were used in the program DIVA-GIS v 7.5 (Hijmans et al. 2001) to infer general geology from the digital version of the 1:750,000 Geologic Map of California (Jennings et al. 1977; Saucedo et al. 2000). Local geology was inferred by visual examination of higher resolution physical or digital maps, including the Geological Maps of the Otay Mesa, La Mesa, and Jamul 7.5′ Quadrangles (Kennedy and Tan 1977). Local soils were inferred using data from the Soil Survey Geographic (SSURGO) database for San Diego County, California, obtained from the United States Department of Agriculture Natural Resource Conservation Service (USDA 2007).

Soil Sampling

To quantify the soil chemistry associations of *C. otayensis* and closely related members of *Ceanothus* subg. *Cerastes*, soils were collected from 29 plant populations in California (Table 2, Fig. 1). The aim of this sampling was to obtain soils from as many *C. otayensis* populations as possible, and from a representative diversity of soils occupied by other members of *Ceanothus* subg. *Cerastes*. For the species other than *C. otayensis*, an effort was made to maximize the diversity of substrates represented in the dataset, and to sample from as many purported edaphic-endemic taxa as possible. (Wilken 2006). Seven of the resulting samples were from populations or subpopulations of *C. otayensis* (5 metavolcanic from the San Ysidro Mountains; 2 sedimentary, from MCAS Miramar), and 22 were from species other than *C. otayensis*, representing 13 of the 23 currently recognized members of *Ceanothus* subg. *Cerastes* (Wilken 2006) and all but one of the approximately eight edaphic-endemic members of this group (Table 2, Figs. 1 and 2). Sampling of soil was carried out in April and May 2009, and again in April 2013. The soil sampling procedure follows that of Burge and Manos (2011).

Soil Chemistry Assays

Soil chemistry analyses were done by the Texas A&M University Soil, Water, and Forage Testing Laboratory. Methods were as described by Burge and Manos (2011). In all, 13 soil properties were assayed (Table 3), including pH, nitrate (NO_3^-), electrical conductivity, major nutrients (P, K, Ca, Mg, and S), micronutrients (Cu, Fe, Mn, and Zn), and sodium (Na).

Analysis of Soil Chemistry Data

Soil chemistry data were treated in a multivariate statistical framework. Differences between sedimentary (MCAS Miramar; n = 2) and metavolcanic (San Ysidro Mountains; n = 5) soils of *C. otayensis*, as well as differences between the soils of *C. otayensis* and other species of *Ceanothus* subg. *Cerastes* from California (n = 22), were summarized and tested using principal component analysis (PCA) and generalized canonical discriminant analysis (Gittins 1985). Principal components analysis was done in R version 2.10.1 (R Development Core Team 2013), using the "ecodist" package of Goslee and Urban (2007). Soil chemistry variables were transformed into Z-scores before analysis. Following analysis, the first two principal components were visualized in bivariate space and the contribution of different soil chemistry variables to the components was assessed using vector loading. Generalized

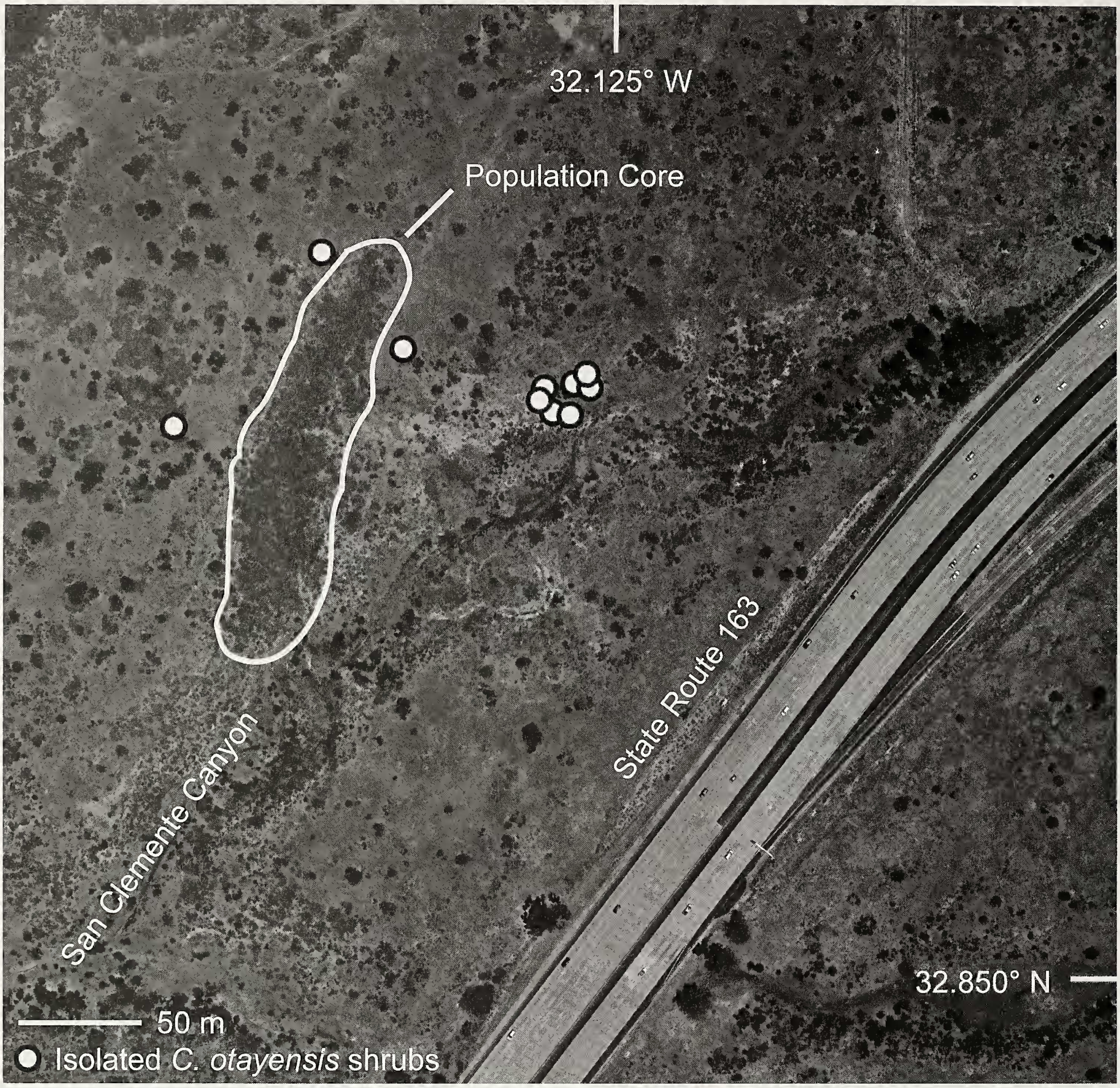

FIG. 3. Distribution of *C. otayensis* at MCAS Miramar. Map shows detail of upper (eastern) San Clemente Canyon, with core population of *C. otayensis* and outlying individuals. Background image from USGS (2012).

canonical discriminant analysis was done in R (R Development Core Team 2013), using the "candisc" package of Friendly and Fox (2009). Wilks' Lambda was used to test for significant differences between the two groups based on the 13 soil chemistry variables (Friendly 2007).

Estimation of Population Size at MCAS Miramar

A transect approach was used to estimate the size of the *C. otayensis* population at its disjunct locality on MCAS Miramar. With the exception of a few outlying shrubs, *C. otayensis* at MCAS Miramar is restricted to a patch of extremely dense chaparral at the head of a tributary of San Clemente Canyon (Fig. 3). Because this patch is surrounded by open scrub, it was possible to walk the perimeter of the patch and count individual adult plants. Two observers (DOB and K. Zhukovsky) walked the margin of the chaparral patch (Fig. 3), pausing approximately every 5 m to tally the number of new individuals observable in a line across the canyon. In addition, the surrounding portions of Kearny Mesa and upper San Clemente Canyon were explored on foot (Fig. 3), and additional outlying individuals of *C. otayensis* were noted. The position of isolated individuals was recorded using a hand-held GPS and the WGS84 datum. All work for the population size estimate was carried out on 18 April 2013.

Results

Geological Formations and Soil Types

Using the CCH database and collections obtained specifically for this project, 19 unique *C. otayensis* localities were identified (CCH 2013, Appendix 2). Fourteen of these are in the Peninsular Ranges of southern San Diego County, California and northern Baja California, Mexico (San Ysidro Mountains and San Miguel Mountain; Fig. 1), and two are at the recently discovered locality at MCAS Miramar in northern San Diego County. Inferred geological and soil formations for these sites (Appendix 2) indicate that three major groupings of sites are present (Table 1): 1) localities at MCAS Miramar, 2) localities on San Miguel Mountain and the California portion of the San Ysidro Mountains, and 3) one locality in northern Baja California, Mexico, in the southernmost San Ysidro Mountains (Fig. 1). At the first set of localities, rocks are classified as sedimentary; soils are classified as Terrace escarpments and Redding gravelly loam (Appendix 2; Table 1). At the second set of localities, by contrast, the rocks are classified as volcanic or metavolcanic; soils are classified as San Miguel-Exchequer rocky silt loams and metamorphic rock land (Table 1). The final locality, from Baja California, Mexico, is apparently on soils derived from andesite, a volcanic rock type (Appendix 1; Table 1). However, this rock is likely metavolcanic, based on the geological setting and field observations by the author (2009).

Soil Chemistry

In comparison to the soils of other *Ceanothus* species assayed, the soils of *C. otayensis* have, on average, lower pH, lower electrical conductivity, lower concentrations of nitrate, and lower levels of every assayed nutrient other than potassium, sodium, zinc, and manganese (Table 3). These differences are significant in the case of conductivity, nitrate, sulfur, and sodium (Student's paired t-tests, $P < 0.03$). In comparison to *C. otayensis* from metavolcanic soils of the San Ysidro Mountains ($n = 5$), the soils of *C. otayensis* from MCAS Miramar ($n = 2$) have nearly identical levels for all of the assayed chemical properties (Table 3); there were no significant differences for any of these properties (Student's paired t-tests, $P > 0.05$).

Principal components analysis and canonical discriminant analysis provide a summary of the results for the 13 soil chemistry variables (Fig. 4). In the case of PCA, the first two principal components account for 50% of variance, with 30% on the first principal component and 20% on the second. The first principal component is strongly positively correlated with conductivity (vector loading = 0.45) and iron (vector loading = 0.44), and strongly negatively correlated with phosphorous (vector loading = −0.13).

In canonical discriminant analysis, three groups (1, *C. otayensis* MCAS Miramar; 2, *C. otayensis* San Ysidro Mountains; and 3, other species; Table 2) were used to transform soil chemistry variables into canonical space (Fig. 5). A single coordinate axis accounted for 100% of the variance, and the Wilks' Lambda test (approximate $F = 4.06$) allowed for rejection of the null hypothesis of no difference between the means for the three groups ($P = 0.005$). Examination of the canonical discriminant plot (Fig. 5) indicates that this pattern is driven by the difference in chemistry between soils of *C. otayensis* and the other species. To test this, a two-tailed t-test was carried out using vector loadings from the first and second principal components of the PCA (Fig. 4), using the two *C. otayensis* localities (MCAS Miramar and San Ysidro Mountains) as groups. This test indicated that the two groups are not distinguishable on the basis of the first or second principal component axes ($P = 0.95$ and $P = 0.39$, respectively).

Population Size at MCAS Miramar

A total of 74 individual shrubs of *C. otayensis* were observed during the transect work (Fig. 3). All individuals were mature, many of them in heavy fruit at the time of observation. No seedlings were observed. Many of the *C. otayensis* individuals were senescent. A few isolated individuals of *C. otayensis* were observed in the vicinity of the core population at the head of San Clemente Canyon (Fig. 3; *Burge 1378*; Appendix 1; Table 2), but no other populations were located at MCAS Miramar.

Discussion

Soils of *C. otayensis* from the two disjunct population centers (Figs. 1 and 2; San Ysidro Mountains and MCAS Miramar) are chemically indistinguishable (Fig. 5), which is surprising given the very different geological origin of these materials (Table 2); those from the San Ysidro Mountains region have arisen from metavolcanic rocks, while those from MCAS Miramar are from sedimentary rocks, including Quaternary alluvium and more ancient conglomerate (Appendix 2). The chemical similarity of these soils may help to explain the disjunct occurrence of *C. otayensis* at MCAS Miramar, 25 km northwest of other known populations (Figs. 1 and 2).

Substrate Associations

Results presented here indicate that edaphic conditions experienced by *C. otayensis* represent a cohesive and distinctive subset of conditions

TABLE 1. ROCK AND SOIL TYPES FOR 19 *C. OTAYENSIS* LOCALITIES. *Group* refers to the three general groupings of localities mentioned in the body of the paper (Fig. 1). *Region* refers to geographic regions (Fig. 1). *Collection number* refers to the herbarium sheet upon which the record is based (Appendix 2). *General geology* is from the Geologic Map of California (Jennings et al. 1977); data for Burge 1063 is from Reconnaissance Geology of the State of Baja California (Gastil et al. 1971). *Local geology* is from Geology of La Mesa, Jamul, and Otay Mesa 7.5′ Quadrangles (Kennedy et al. 1977); local geology data for some San Ysidro Mountains localities are not available, but are likely to be the same as the other localities from this mountain range. *Soil* is from the Soil Survey Geographic (SSURGO) database for San Diego County. Some data are not available for *Burge 1063*.

Group	Region	Collection number	General geology	Local geology	Soil
1	MCAS Miramar	*Burge 1179*	Sedimentary (Ec)	Lindavista Formation (Ql)	Terrace escarpments (TeF)
	MCAS Miramar	*Burge 1398*	Sedimentary (Ec)	Lindavista Formation (Ql)	Redding gravelly loam (RdC)
2	N. San Ysidro Mts.	*Moran 17863*	Volcanic (Mzv)	Metavolcanic (KJmv)	Metamorphic rock land (MrG)
	N. San Ysidro Mts.	*Moran 23785*	Volcanic (Mzv)	Metavolcanic (KJmv)	San Miguel-Exchequer rocky silt loams (SnG)
	N. San Ysidro Mts.	*Pratt s.n.*	Volcanic (Mzv)	Metavolcanic (KJmv)	San Miguel-Exchequer rocky silt loams (SnG)
	N. San Ysidro Mts.	*Pierce s.n.*	Volcanic (Mzv)	Metavolcanic (KJmv)	San Miguel-Exchequer rocky silt loams (SnG)
	N. San Ysidro Mts.	*Elvin 1306*	Volcanic (Mzv)	Metavolcanic (KJmv)	San Miguel-Exchequer rocky silt loams (SnG)
	N. San Ysidro Mts.	*Rebman 6742*	Volcanic (Mzv)	Metavolcanic (KJmv)	San Miguel-Exchequer rocky silt loams (SnG)
	N. San Ysidro Mts.	*Sanders 26436*	Volcanic (Mzv)	Metavolcanic (KJmv)	San Miguel-Exchequer rocky silt loams (SnG)
	N. San Ysidro Mts.	*Betzler 515*	Volcanic (Mzv)	Metavolcanic (KJmv)	San Miguel-Exchequer rocky silt loams (SnG)
	N. San Ysidro Mts.	*Rebman 11043*	Volcanic (Mzv)	Metavolcanic (KJmv)	San Miguel-Exchequer rocky silt loams (SnG)
	N. San Ysidro Mts.	*Burge 983*	Volcanic (Mzv)	Metavolcanic (KJmv)	Metamorphic rock land (MrG)
	N. San Ysidro Mts.	*Burge 985*	Volcanic (Mzv)	Metavolcanic (KJmv)	Metamorphic rock land (MrG)
	N. San Ysidro Mts.	*Burge 1053*	Volcanic (Mzv)	Metavolcanic (KJmv)	San Miguel-Exchequer rocky silt loams (SnG)
	N. San Ysidro Mts.	*Burge 1391*	Volcanic (Mzv)	Metavolcanic (KJmv)	San Miguel-Exchequer rocky silt loams (SnG)
	N. San Ysidro Mts.	*Burge 1395*	Volcanic (Mzv)	Metavolcanic (KJmv)	Metamorphic rock land (MrG)
	San Miguel Mtn.	*Keeley 27112*	Volcanic (Mzv)	Metavolcanic (KJmv)	San Miguel-Exchequer rocky silt loams (SnG)
	San Miguel Mtn.	*Rebman 24367*	Volcanic (Mzv)	Metavolcanic (KJmv)	San Miguel-Exchequer rocky silt loams (SnG)
3	S. San Ysidro Mts.	*Burge 1063*	Volcanic (Tpa)*	–	–

TABLE 2. SOIL SAMPLING. *Species* from Fross and Wilken (2006); *Code* D. O. Burge collecting code; *Locality* country, state, and county for sampling (also see Appendix 1); all collections by DOB, all deposited at DUKE; *Soil Type* geological material from which soil is derived, with codes from Geological Map of California in parentheses (Jennings et al. 1977).

Species	Code	Locality	Elevation (m)	Geology
C. cuneatus	847	USA; San Luis Obispo Co., CA	310	Ultramafic (um)
	891	USA; Monterey Co., CA	50	Sedimentary (Q, M)
	918	USA; Santa Cruz Co., CA	240	Sedimentary (M)
	982	USA; Riverside Co., CA	730	Granite (grMz)
	984	USA; San Diego Co., CA	1000	Granite (grMz)
	1030	Mexico; Sierra San Pedro Martír	855	Granite (grMz)
	1070	USA; San Bernardino Co., CA	460	Sedimentary (Q)
	1071	USA; Los Angeles Co., CA	615	Granite (grMz)
	1132	USA; Kern Co., CA	1060	Granite (grMz)
	1263	USA; Santa Barbara Co., CA	155	Sedimentary (Q)
C. divergens	833	USA; Sonoma Co., CA	200	Ultramafic (um)
C. divergens	943	USA; Lake Co., CA	1000	Volcanic (Qv)
C. ferrisae	835	USA; Santa Clara Co., CA	180	Ultramafic (um)
C. fresnensis	1138	USA; Fresno Co., CA	1710	Granite (grMz)
C. gloriosus	907	USA; Marin Co., CA	220	Granite (grMz)
C. jepsonii	900	USA; Tehama Co., CA	1200	Ultramafic (um)
C. maritimus	887	USA; San Luis Obispo Co., CA	23	Sedimentary (Q)
C. masonii	913	USA; Marin Co., CA	450	Sedimentary (Kjfm, Mzv)
C. ophiochilus	798	USA; Riverside Co., CA	660	Granite (grMz)
C. otayensis	983	USA; San Ysidro Mts., San Diego Co., CA	900	Volcanic (Mzv)
	985	USA; San Ysidro Mts., San Diego Co., CA	800	Volcanic (Mzv)
	1053	USA; San Ysidro Mts., San Diego Co., CA	430	Volcanic (Mzv)
	1179	USA; MCAS Miramar, San Diego Co., CA	130	Sedimentary (Ec)
	1391	USA; San Ysidro Mts., San Diego Co., CA	690	Volcanic (Mzv)
	1395	USA; San Ysidro Mts., San Diego Co., CA	1016	Volcanic (Mzv)
	1398	USA; MCAS Miramar, San Diego Co., CA	130	Sedimentary (Ec)
C. perplexans	795	USA; San Diego Co., CA	950	Granite (grMz)
C. purpureus	905	USA; Napa Co., CA	410	Volcanic (Tv)
C. roderickii	1288	USA; El Dorado Co., CA	340	Gabbro (gb)

from those supporting other *Ceanothus* species in California and adjacent Mexico (Fig. 4). Soils of *C. otayensis* contain notably small amounts of nitrate and P, low availability of which is known to result in disorders affecting the growth and reproduction of crop plants (Brady and Weil 2002). The soils also have low pH and conductivity, which is probably due to generally low levels of nutrient and other ions (Table 3).

Geospatial data on geological formations and soil types show that the geology and soils of *C. otayensis* from the San Ysidro Mountains and San Miguel Mountain are highly consistent (Table 2; Appendix 2), with metavolcanic geology giving rise to soils from two series, the San Miguel-Exchequer rocky silt loams and Metamorphic rock land. Metavolcanic rocks of the San Ysidro Mountains and San Miguel Mountain are part of

TABLE 3. SUMMARY STATISTICS FOR SOIL CHEMISTRY VARIABLES. *Ceanothus otayensis* San Ysidro Mts., n = 5; *Ceanothus otayensis* MCAS Miramar, n = 2; Other *Ceanothus* species, n = 22; all variables reported as average plus or minus standard deviation; conductivity reported as µmol/cm; nitrate and all other levels reported as ppm.

Variable	*Ceanothus otayensis* San Ysidro Mts.	*Ceanothus otayensis* MCAS Miramar	Other *Ceanothus* species
pH	5.91 ± 0.20	5.46 ± 0.21	6.03 ± 0.72
Conductivity	68 ± 25	67 ± 7.07	127.46 ± 115.55
Nitrate	2.01 ± 1.46	1.32 ± 1.12	12.42 ± 17.83
P	6.49 ± 1.08	8.78 ± 4.10	28.40 ± 35.15
K	203.34 ± 59.55	204.87 ± 50.92	172.92 ± 96.56
Ca	1197.84 ± 369.56	967.48 ± 81.31	1222.10 ± 721.59
Mg	201.33 ± 51.58	237.70 ± 42.52	697.86 ± 1091.01
S	6.02 ± 1.83	6.73 ± 0.99	10.91 ± 3.79
Na	35.32 ± 3.89	33.58 ± 1.75	81.26 ± 63.56
Fe	10.25 ± 3.08	17.86 ± 5.96	23.03 ± 14.90
Zn	0.60 ± 0.41	1.50 ± 0.34	0.88 ± 1.27
Mn	9.37 ± 2.66	13.38 ± 2.25	10.68 ± 7.14
Cu	0.14 ± 0.04	0.34 ± 0.05	0.38 ± 0.30

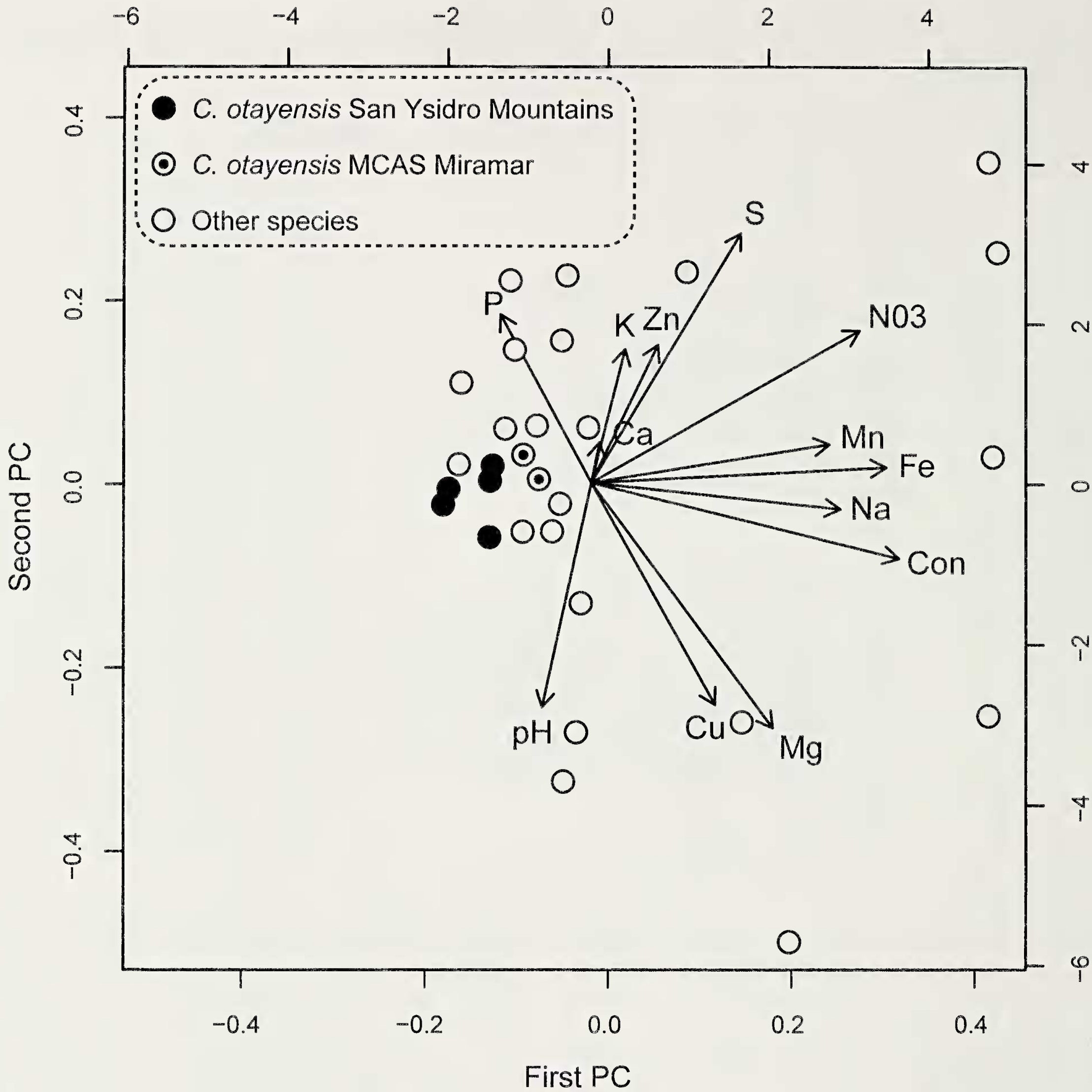

FIG. 4. Plot from principal components (PCA) analysis of soil chemistry. Biplot for first two principal components of PCA for 29 soil samples. Arrows represent direction and magnitude of loading on principal component axes. Symbols: Con = electrical conductivity; N03 = nitrate.

a narrow band of such geological materials extending northward from northern Baja California, Mexico into San Diego County, including some minor peaks and uplands to the west and northwest of San Diego (e.g., Black Mountain).

Metavolcanic-derived soils of the San Ysidro Mountains and San Miguel Mountain are known to host a diverse flora and a number of near-endemics, such as *Arctostaphylos otayensis* Wies. & Schreib. (Ericaceae), *Lepechinia ganderi* Epling (Lamiaceae), *Hosackia crassifolius* Benth. var. *otayensis* (Moran ex Isely) Brouillet (Fabaceae), and notable populations of other rare species, such as *Brodiaea orcuttii* (Greene) Baker (Themidaceae), *Calochortus dunnii* Purdy (Liliaceae), *Stipa diegoensis* Swallen (Poaceae), *Fremontodendron mexicanum* Davidson (Sterculiaceae), *Quercus cedrosensis* C.H. Muller (Fagaceae), and *Hesperocyparis forbesii* (Jeps.) Bartel (Cupressaceae). Many of these species are also known from gabbro-derived soils of San Diego County, which often support a unique suite of rare species (Zedler 1995, Alexander 2011). The presence of these rare taxa on both metavolcanic and gabbro rock suggests that there may be some chemical similarity between soils derived from this material, as the present paper shows for the metavolcanic-derived and sedimentary soils of *C. otayensis*. Future work should compare the substrate associations of these species. Such work would likely aid in the management of these rare and poorly-known taxa.

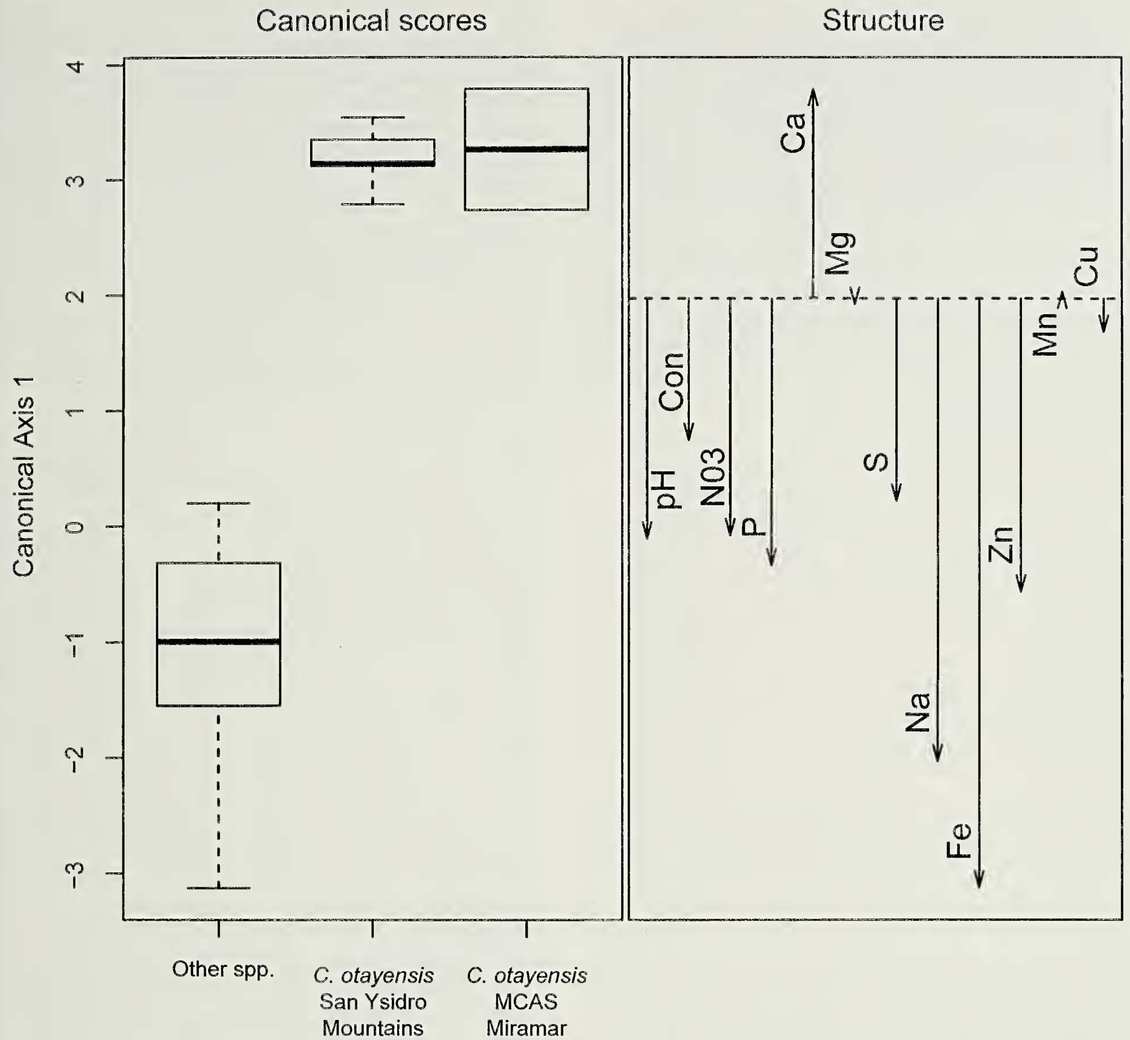

FIG. 5. Results of PCA Plot from generalized canonical discriminant analysis (CDA) of soil chemistry. Plot of single canonical axis from CDA comparing means of 1) *C. otayensis* from MCAS Miramar, 2) *C. otayensis* from the San Ysidro Mountains, and 3) other *Ceanothus* species. Symbols: Con = electrical conductivity; N03 = nitrate.

Sedimentary soils like those at the MCAS Miramar locality are also known to support a diverse and unusual flora, possibly due to the low pH that prevails on some soils (Crocker 1956). However, most of these species are vernal-pool endemics or associates. *Ceanothus otayensis*, a shrub normally associated with chaparral habitats, thus provides an unusual counterpoint to the typical pattern of endemic plant diversity at MCAS Miramar. Although additional research is clearly needed, particularly targeted surveys of plant diversity in and near MCAS Miramar, there are some intriguing examples of other plants disjunct between MCAS Miramar and the San Ysidro Mountains; the endangered herb *Monardella viminea* Greene is found on MCAS Miramar and a few other scattered localities in San Diego County and adjacent Baja California, Mexico, while the closely related *Monardella stoneana* Elvin & A.C. Sanders is found only on metavolcanic soils of the San Ysidro Mountains. It is possible that other examples of this disjunction exist, but have not been detected by botanists. The present study shows that there is a chemical similarity between the soils of *C. otayensis* from the San Ysidro Mountains and those at MCAS Miramar, which in turn suggests that other plants of the San Ysidro Mountains, or other rare plants of southern San Diego County, might be expected to occur there. Such examples of disjunction due to soil cross-tolerance are well known in the botanical literature (reviewed in Brady et al. 2005), but few cases have been examined in a soil chemistry or experimental context.

In considering the ecology of *C. otayensis* and other rare plants from the region of the border between Mexico and the Unites States, it is important to also consider populations from Baja California, Mexico. In the case of *C. otayensis*, a population of the species is known to occur near the summit of Cerro Jesús María in Baja California, one of the southern peaks of the San Ysidro Mountains (Fig. 1). Here, it appears to occur on andesite-derived (volcanic) soils (Appendix 1). It would be helpful to obtain soil samples from this locality for future work involving the evolution and ecology of *C. otayensis*. It would also be helpful to analyze soil samples from the populations of plants that have been reported from San Miguel Mountain in San Diego County (*Keeley 27100-27117*, *Rebman* 24367; Appendix II).

Evolution of Soil Specificity

Although my work does not directly address the evolutionary history of the new, disjunct *C. otayensis* population on Kearney Mesa at MCAS Miramar, it is possible to speculate on the historical events that may have led to the present distribution of the species. One possibility is that the population at MCAS Miramar is the product of a recent dispersal event from the south, and has been able to persist in the new, unusual habitat due to the amenable chemistry of the soils. Alternatively, plants at MCAS Miramar may be relictual, isolated by the loss of plant populations in the region separating MCAS Miramar from the San Ysidro Mountains and San Miguel Mountain. It is intriguing to note that metavolcanic rocks, as well as sedimentary formations of the same type found at the MCAS Miramar locality, are broadly distributed in a continuous band from the San Ysidro Mountains region to north of MCAS Miramar (Fig. 2). It is possible that some of these areas support other small, undiscovered populations of *C. otayensis*.

The soils of *C. otayensis* are chemically similar to soils that support another narrowly-endemic *Ceanothus* species, *Ceanothus roderickii* Knight, which is known from gabbro-derived soils of the central Sierra Nevada (Fig. 4; Burge and Manos 2011). Recent research on *C. roderickii* indicates that the chemistry of its soils may provide a powerful agent of natural selection, possibly leading to reduced gene flow with closely related species, local adaptation, and speciation (Burge et al. 2013). If this hypothetical mode of divergence and speciation is common in *Ceanothus*, it may help explain the origin of *C. otayensis*, as well as several other narrowly-endemic *Ceanothus* species from southern California and nearby Baja California, including *Ceanothus ophiochilus* S. Boyd, T. S. Ross, & Arnseth on pyroxenite-rich gabbros of Riverside County (Boyd and Arnseth 1991), and *Ceanothus bolensis* S. Boyd & J. Keeley on metavolcanic rocks of Baja California's Cerro Bola (Boyd et al. 2002).

In general, it would be worthwhile to make a broader test of soil chemistry associations across the ten or so supposedly edaphic-endemic members of *Ceanothus* subg. *Cerastes*, to determine whether there is a consistent syndrome of edaphic adaptation across the group. Such work should ideally include common garden experiments, reciprocal transplant experiments, and more detailed analyses of other soil parameters that are potentially related to the chemical parameters, such as moisture availability. This would help to overcome the limitations of this and many similar studies, which often rely on purely observational data from a small suite of chemical soil properties.

Status of the New Population and of the Species

Ceanothus otayensis is on list 1B.2 of the California Native Plant Society Inventory of Rare and Endangered Plants (CNPS 2014), meaning that it is rare in California as well as in its other areas of distribution (in this case Baja California, Mexico). *Ceanothus otayensis* is facing a number of significant threats throughout its geographic range. The major threat to the persistence of the species is likely fire regime; *C. otayensis* is an obligate seeding species that requires fire for recruitment (Wilken 2006). However, too frequent fire has been shown to eliminate obligate seeding species from chaparral habitats in southern California (Zedler 1995). Major wildfires have burned large portions of the San Ysidro Mountains during the past decade, including the Cedar Fire (ignited 25 October 2003; burned 582 km^2; CAL FIRE 2014), and the Witch Creek Fire (ignited 21 October 2007; burned 801 km^2; CAL FIRE 2014). These were two of the largest fires in the recorded history of California (CAL FIRE 2014), and both burned substantial portions of *C. otayensis* habitat in the San Ysidro Mountains and nearby Peninsular Ranges, including portions in Baja California, Mexico. Short fire intervals of this kind will probably result in the extirpation of *C. otayensis* populations that are unable to reach sexual maturity between fires.

Though populations of *C. otayensis* in the San Ysidro Mountains are large and seem reasonably secure, the smaller populations at San Miguel Mountain and MCAS Miramar could suffer drastic losses in the event of future fires. For example, virtually the whole of San Miguel Mountain was burned in the 2007 Witch Creek Fire (CAL FIRE 2014), including the portion of the mountain where *C. otayensis* was most recently recorded (*Keeley 27100–27117*, *Rebman 24367*; Appendix 1).

As discussed above, the new record of the species from MCAS Miramar represents a significant expansion of the ecological and geographic range known for the species. The new locality at MCAS Miramar brings the total number of population centers for the species to three, one in the San Ysidro Mountains, a second on San Miguel Mountain, and a third, now, at MCAS Miramar (Fig. 1). Nevertheless, the population at MCAS Miramar is extremely small, seemingly consisting of no more than 74 mature plants. Although the size of the nearest *C. otayensis* population on San Miguel Mountain is also very small (probably no more than 100 individuals as of 2010, Jon Rebman personal communication), population sizes in the San Ysidro Mountains are generally significantly larger, consisting of thousands of plants, becoming a co-dominant member of the chaparral plant community at higher elevations. The very small size of the *C. otayensis* population at MCAS Miramar makes it especially vulnerable to loss. In such populations, chance events such as wildfire, flooding, or disease introduction can lead to drastic losses of individuals, and possibly local extinction. In addition, the population genetic status of this small population is unknown. If the population is derived via a recent dispersal event from the southern populations, it may suffer from a lack of genetic diversity due to a population bottleneck (Ellstrand and Elam 1993). On the other hand, if the plant at MCAS Miramar is a relictual population, isolated by the loss of plant populations in the region separating Kearny Mesa from the San Ysidro Mountains, it may harbor unique genetic variation not present in the southern populations. Future work should aim to quantify population genetic variation across the range of *C. otayensis*, especially in isolated population centers, such as those at MCAS Miramar and San Miguel Mountain.

Acknowledgments

The author thanks Katherine Zhukovsky, Jon Rebman, and Dieter Wilken for providing constructive criticism of drafts. Assistance with field work and field logistics was provided by Katherine Zhukovsky, JoEllen Kassebaum, and Joyce Schlachter. Funding was provided by the American Society of Plant Taxonomists, The Hunt Institute for Botanical Documentation, Duke University, and a National Science Foundation grant to DOB and PSM (NSF 000457253).

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Appendix 1

Sampled *Ceanothus* Populations.

For each sampled population (see Table 2), the format is as follows: collector name and number (herbarium of voucher specimen deposition), description of locality, county, US or Mexican state.

Ceanothus cuneatus **(Hook.) Nutt.**—*D.O. Burge 847* (DUKE), Irish Hills Natural Reserve, San Luis Obispo Co., CA. *D.O. Burge 891* (DUKE), Fort Ord Military Reservation, Monterey Co., CA. *D.O. Burge 918* (DUKE), Henry Cowell Redwoods State Park, Santa Cruz Co., CA. *D.O. Burge 982* (DUKE), Tucalota Creek watershed, Riverside Co., CA. *D.O. Burge 984* (DUKE), Morena Valley, San Diego Co., CA. *D.O. Burge 1030* (DUKE), Sierra San Pedro Martir, Baja California, Mexico. *D.O. Burge 1070* (DUKE), Rialto Municipal Airport, San Bernardino Co., CA. *D.O. Burge 1071* (DUKE), Sierra Pelona Mountains, Ruby Canyon, Los Angeles Co., CA. *D.O. Burge 1132* (DUKE), Clear Creek watershed, south of Ball Mountain, Kern Co., CA. *D.O. Burge 1263* (DUKE), Solomon Hills, north of Graciosa Ridge, Santa Barbara Co., CA.

Ceanothus divergens **Parry**—*D.O. Burge 833* (DUKE), Southeast flank of Mount Hood, Sonoma Co., CA. *D.O. Burge 943* (DUKE), Boggs Mountain Demonstration State Forest, Lake Co., CA.

Ceanothus ferrisiae **McMinn**—*D.O. Burge 835* (DUKE), Anderson Lake County Park, Santa Clara Co., CA.

Ceanothus fresnensis **Dudley ex Abrams**—*D.O. Burge 1138* (DUKE), Big Creek Watershed, Fresno Co., CA.

Ceanothus gloriosus **J.T. Howell**—*D.O. Burge 907* (DUKE), Point Reyes National Seashore, Inverness Ridge, Marin Co., CA.

Ceanothus jepsonii **Greene**—*D.O. Burge 900* (DUKE), Mendocino National Forest, at roadside 12.5 road miles (20 km) west of Paskenta, Tehama Co., CA.

Ceanothus maritimus **Hoover**—*D.O. Burge 887* (DUKE), Roadside on Hwy 1, 0.5 road miles (0.8 km) north of bridge over Arroyo de los Chinos, San Luis Obispo Co., CA.

Ceanothus masonii **McMinn**—*D.O. Burge 913* (DUKE), Golden Gate National Recreation Area, Bolinas Ridge, Marin Co., CA.

Ceanothus ophiochilus **S. Boyd, T.S. Ross & Arnseth**—*D.O. Burge 798* (DUKE), Agua Tibia Wilderness Area, Cleveland National Forest, Riverside Co., CA.

Ceanothus otayensis **McMinn**—*D.O. Burge 983* (DUKE), Otay Mountain, 6.6 road miles from Otay Lakes Road via Minewawa and Otay Mountain Truck Trails, San Diego Co., CA. *D.O. Burge 985* (DUKE), Otay Mountain, 7.4 road miles from Otay Lakes Road via Minewawa and Otay Mountain Truck Trails, San Diego Co., CA. *D.O. Burge 1053* (DUKE), San Ysidro Mountains, roadside on Otay Mountain Truck Trail, 1.7 road miles (2.7 km) from Alta Road, San Diego Co., CA. *D.O. Burge 1179* (DUKE), Marine Corps Air Station Miramar, Kearny Mesa, San Diego Co., CA. *D.O. Burge 1391* (DUKE), San Ysidro Mountains, northern slope of Otay Mountain, upper slopes of Little Cedar Canyon, San Diego Co., CA. *D.O. Burge 1395* (DUKE), San Ysidro Mountains, Otay Mountain, Doghouse Junction, San Diego Co., CA. *D.O. Burge 1398* (DUKE), Marine Corps Air Station Miramar, Kearny Mesa, San Diego Co., CA.

Ceanothus perplexans **Trel.**—*D.O. Burge 795* (DUKE), Chariot Canyon, San Diego Co., CA.

Ceanothus purpureus **Jeps.**—*D.O. Burge 905* (DUKE), Atlas Road, Napa Co., CA.

Ceanothus roderickii **W. Knight**—*D.O. Burge 1288* (DUKE), South Fork American River watershed, El Dorado Co., CA.

Appendix 2

Geology and Soil Associations of *C. otayensis*.

For each population, the format is as follows: collector name and number (herbarium of voucher specimen deposition), description of locality, county, US or Mexican state (state geology; local geology; soil). *General geology* for California is from the Geologic Map of California (Jennings et al. 1977); Mexican locality is from Reconnaissance Geology of the State of Baja California (Gastil et al. 1971). *Local geology* is from Geology of La Mesa, Jamul, and Otay Mesa 7.5′ Quadrangles (Kennedy et al. 1977); data for some San Ysidro Mountains localities are not available for these maps, but are likely to be the same as the other San Ysidro Mountains localities, as indicated. *Soil*, is from the Soil Survey Geographic (SSURGO) database for San Diego County.

Ceanothus otayensis—*Moran 17863* (CAS), Summit of Otay Mountain, San Diego Co., CA (state geology: volcanic [Mzv]; local geology: Metavolcanic [KJmv]; soil: Metamorphic rock land [MrG]. *Moran 23785* (RSA), 1 1/2 miles east of Doghouse Junction, Otay Mountain, San Diego Co., CA (state geology: volcanic [Mzv]; local geology: Metavolcanic [KJmv]; soil: San Miguel-Exchequer rocky silt loams [SnG]. *Pratt s.n.* (UCR), Along the main road up Otay Peak, San Diego Co., CA (state geology: volcanic [Mzv]; local geology: Metavolcanic [KJmv]; soil: San Miguel-Exchequer rocky silt loams [SnG]. *Pierce s.n.* (UCR), SW side Otay Mtn, just east of head of Johnson Cyn, San Diego Co., CA (state geology: volcanic [Mzv]; local geology: Metavolcanic [KJmv]; soil: San Miguel-Exchequer rocky silt loams [SnG]. *Elvin 1306* (CAS), West Otay Mountain, north of Otay Truck Trail, San Diego Co., CA (state geology: volcanic [Mzv]; local geology: Metavolcanic [KJmv]; soil: San Miguel-Exchequer rocky silt loams [SnG]. *Rebman 6742* (RSA), West side of Otay Mountain, San Diego Co., CA (state geology: volcanic [Mzv]; local geology: Metavolcanic [KJmv]; soil: San Miguel-Exchequer rocky silt loams [SnG]. *Sanders 26436* (RSA), Otay Mountain, lower 'Copper Canyon', San Diego Co., CA (state geology: volcanic [Mzv]; local geology: Metavolcanic [KJmv]; soil: San Miguel-Exchequer rocky silt loams [SnG]. *Betzler 515* (RSA), Otay Mountain, Minnewawa Truck Trail about 3.5 miles from top, San Diego Co., CA (state geology: volcanic [Mzv]; local geology: Metavolcanic [KJmv]; soil: San Miguel-Exchequer rocky silt loams [SnG]. *Rebman 11043* [RSA], Otay Mountain Ecological Reserve, San Diego Co., CA (state geology: volcanic [Mzv]; local geology: Metavolcanic [KJmv]; soil: San Miguel-Exchequer rocky silt loams [SnG]. *Burge 983* [DUKE], Otay Mountain, 6.6 road miles from Otay Lakes Road via Minewawa and Otay Mountain Truck Trails, San Diego Co., CA (state geology: volcanic [Mzv]; local geology: Metavolcanic [KJmv]; soil: Metamorphic rock land [MrG]). *Burge 985* (DUKE), Otay Mountain, 7.4 road miles from Otay Lakes Road via Minewawa and Otay Mountain Truck Trails, San Diego Co., CA (state geology: volcanic [Mzv]; local geology: Metavolcanic [KJmv]; soil: Metamorphic rock land [MrG]). *Burge 1053* (DUKE), San Ysidro Mountains, roadside on Otay Mountain Truck Trail, 1.7 road miles (2.7 km) from Alta Road, San Diego Co., CA (state geology: volcanic [Mzv]; local geology: Metavolcanic [KJmv]; soil: San Miguel-Exchequer rocky silt loams [SnG]). *Burge 1391* (DUKE), San Ysidro Mountains, northern slope of Otay Mountain, upper slopes of Little Cedar Canyon, San Diego Co., CA (state geology: volcanic [Mzv]; local geology: Metavolcanic [KJmv]; soil: San Miguel-Exchequer rocky silt loams [SnG]). *Burge 1395* (DUKE), San Ysidro Mountains, Otay Mountain, Doghouse Junction, San Diego Co., CA (state geology: volcanic [Mzv]; local geology: Metavolcanic [KJmv]; soil: Metamorphic rock land [MrG]). *Keeley 27112* (RSA), N face of San Miguel Mtn, 8 km SW of Hwy 94 at bridge near Jacumba, San Diego Co., CA (state geology: volcanic [Mzv]; local geology: Metavolcanic [KJmv]; soil: San Miguel-Exchequer rocky silt loams [SnG]). *Rebman 24367* (SD), San Miguel Mountain, east of the Sweetwater Reservoir, along Miller Ranch Road, San Diego Co., CA (state geology: volcanic [Mzv]; local geology: Metavolcanic [KJmv]; soil: San Miguel-Exchequer rocky silt loams [SnG]). *Burge 1179* (DUKE), Marine Corps Air Station Miramar, Kearny Mesa, San Diego Co., CA (state geology: Eocene conglomerate [Ec]; local geology: Lindavista Formation [Ql]; soil: Terrace escarpments [TeF]). *Burge 1398* (DUKE), Marine Corps Air Station Miramar, Kearny Mesa, San Diego Co., CA (state geology: Eocene conglomerate [Ec]; local geology: Lindavista Formation [Ql]; soil: Redding gravelly loam [RdC]). *Burge 1063* (DUKE), San Ysidro Mountains, Cerro Jesús María, Baja California, Mexico (Geology: Andesite [Tpa]).